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RESEARCH ARTICLE

The predominant role of soil in determining species composition of fern communities in subtropical coastal forest ecosystems

O papel predominante do solo na determinação da composição de espécies de comunidades de samambaias em ecossistemas de florestas costeiras subtropicais

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Abstract

Ferns are an important component in the understorey of tropical forests and their distribution is influenced by several biotic and abiotic factors. At a regional scale, soil characteristics and canopy openness play an important role in fern species composition and richness, as well as in the abundance of individuals. Our objective was to compare the influence of edaphic conditions and vegetation structure on the abundance and distribution of fern communities in Atlantic forest and *restinga* forest. Our hypotheses were that fern species richness and diversity are higher in Atlantic forest than in *restinga* due to limiting conditions in this habitat and the composition of fern species in Atlantic forest differs from *restinga*, especially due to differences in edaphic conditions. A principal coordinates analysis was applied to ordinate sampling units in relation to the environmental variables and a permutational multivariate

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analysis of variance was used to test that environmental variables did not differ between the two vegetation types. Species richness was compared using rarefaction curves. The influence of abiotic variables in species composition and abundance was verified using canonical correspondence analysis. No differences were observed in species richness, diversity or dominance between vegetation types, although abundance was higher in *restinga*. Fern communities respond to edaphic conditions and vegetation structure variations between vegetation types, the soil playing a major role. A greater variety of habitats resulting from differences in soil drainage in *restinga* facilitates the co-existence of species with different ecological tolerance, increasing local diversity and compensating for limiting conditions in *restinga*.

Resumo

Samambaias são um importante componente do subosque das florestas tropicais e sua distribuição está condicionada a diversos fatores bióticos e abióticos. Em escala regional, características do solo e da abertura do dossel exercem importante papel na composição e riqueza de espécies de samambaias, bem como na abundância dos indivíduos. O objetivo do estudo foi comparar a influência das condições edáficas e da estrutura da vegetação na abundância e distribuição de comunidades de samambaias na floresta Atlântica e na floresta de restinga. As hipóteses foram que a riqueza de espécies e a diversidade de samambaias são maiores na floresta Atlântica do que na restinga devido às condições limitantes neste habitat e, a composição de espécies de samambaias na Mata Atlântica difere da restinga especialmente devido à diferenças nas condições edáficas. Uma análise de coordenadas principais foi aplicada, para ordenar unidades amostrais em relação às variáveis ambientais, e uma análise de variância multivariada permutacional foi usada para testar se as variáveis ambientais não diferiram entre os dois tipos de vegetação. A riqueza de espécies foi comparada usando curvas de rarefação. A influência das variações abióticas na composição e abundância das espécies foi verificada por meio da análise de correspondência canônica. Não foram observadas diferenças na riqueza, diversidade ou dominância entre os tipos de vegetação, embora a abundância tenha sido maior na restinga. As comunidades de samambaias respondem às condições edáficas e às variações da estrutura da vegetação entre os dois tipos de vegetação, tendo o solo um papel importante. A maior variedade de habitats decorrentes das diferenças na drenagem do solo na restinga facilita a coexistência de espécies com diferentes tolerâncias ecológicas, aumentando a diversidade local e compensando as condições limitantes na restinga.

Keywords

abiotic factors, Brazil, canopy cover, diversity, dominance, nutrient richness, vegetation structure

Palavras-chave

fatores abióticos, Brasil, cobertura do dossel, diversidade, dominância, riqueza de nutrientes, estrutura da vegetação

Introduction

Ferns are cosmopolitan, occurring in virtually all tropical, temperate and semi-arid ecosystems (Sharpe et al. 2010). At the global level, climate exerts a great influence on the distribution and abundance of ferns. The diversity of the group is positively correlated with the increase in temperature and moisture from the poles to the tropics on a global scale (Tryon 1986). On a regional scale, soil (Karst et al. 2005; Jones et al. 2013), topography (Moran 1995; Karst et al. 2005), canopy openness (Zuquim et al. 2012; Li et al. 2015), soil drainage (Young and Leon 1989) and vegetation structure (Bittner and Breckle 1995) are the main factors affecting fern communities.

Soils with higher clay content, moisture, organic matter and exchangeable cations tend to support more fern species, while in limiting edaphic conditions, such as high aluminium content (Nóbrega et al. 2011) or water saturation (Young and Leon 1989), the occurrence of ferns is limited to those species better adapted to such conditions (Assis et al. 2011). There seems to be a positive correlation between fern species abundance, soil drainage and litter depth (Tuomisto and Ruokolainen 1993; Tuomisto et al. 2002) and a negative correlation with aluminium content (Nóbrega et al. 2011). Soil texture might also play an important role in the species composition of fern communities (Tuomisto and Ruokolainen 1993; Silva et al. 2013). The reason is that soil granularity interferes in other soil characteristics which influence species composition, such as cation availability (Tuomisto et al. 1998; Nóbrega et al. 2011) and soil moisture (Tuomisto and Ruokolainen 1993).

Changes in canopy openness and composition also exert influence on the fern communities in the understorey. For instance, high light incidence has negative effects on most ferns (Jones et al. 2006). Ferns have high photosynthetic capacity in habitats with low incidence of light and high resistance to phytopathologies common to moist environments (Page 2002), which favours their survival in shaded habitats. Increases in canopy openness allow higher light intensity in the forest floor, reducing local moisture and limiting the growth of many fern species (Paciencia and Prado 2005), especially those less tolerant to dehydration (Page 2002). Canopy openness, therefore, influences species composition and reduces richness and abundance of fern species in sites with higher incidence of light (Jones et al. 2006; Li et al. 2015).

Atlantic forests and *restinga* forests (*restinga* hereafter) are part of the vegetation types in the Atlantic Forest biodiversity hotspot (Myers et al. 2000). *Restinga* develops on predominantly sandy soils with low capacity for water and cation retention, while Atlantic forest develops on soils with higher clay content (Oliveira et al. 1992) and nutrient availability. The aim of this study was to investigate how abiotic factors affect species abundance, richness and composition in fern communities in remnants of Atlantic forest and *restinga* in the Atlantic Forest biome in southern Brazil. The following hypotheses were tested: (1) fern species richness and diversity are higher in Atlantic forest than in *restinga* due to limiting conditions (low water and nutrient availability, high aluminium saturation) in this habitat and, (2) the composition of fern species in Atlantic forest differs from *restinga* especially due to differences in edaphic conditions.

Methods

Study area

This study was conducted in Lagoa do Peri Municipal Park (27°42'41"–27°46'29"S and 48°30'06"–48°33'34"W), Lagoa da Conceição Dunes Municipal Park (27°36'24"–27°38'39"S and 48°26'49"–48°28'05"W) and Lagoa Pequena natural heritage site (27°39'24"–27°39'35"S and 48°28'34"–48°28'20"W) (Florianópolis, southern Brazil) (Fig. 1). The regional climate is humid mesothermal (Peel et al. 2007), with annual

average temperature 19 °C and well distributed rainfall throughout the year averaging 1,500 mm (Pandolfo et al. 2002). The Lagoa do Peri Municipal Park protects remnants of *restinga* and Atlantic forest. The *restinga* vegetation in the other areas is either herbaceous, shrubland or forest, varying with environmental conditions.

Lowland Atlantic forests develop on areas between 5 and 30 m a.s.l. on coastal plains (IBGE 2012). This forest is composed of wide crown trees 15 or 20 m high (Sevegnani 2002). The tree species characteristic of this forest type are mainly in the families Myrtaceae, Euphorbiaceae and Lauraceae (Klein 1980). The Atlantic forest develops mostly on Argisols and Latosols (IBGE 2015). The predominant soil type in the study area is Argisol, originated from physical and chemical weathering of the "island" granite type, resulting in shallow soils of clayey texture and high acidity (Cabral 1999).

Restinga is composed of well developed herbaceous and shrub layers, as well as trees 5 to 15 m high, depending on substrate conditions and the influence of salinity (Guedes-Silva et al. 2005), at sea level or slightly above. Besides holding a vast array of epiphytes and climbers, the most common tree species in *restinga* are in the families Myrtaceae, Fabaceae and Lauraceae (Falkenberg 1999). *Restinga* develops on Neosols, common along the Brazilian coast (IBGE 2015). The predominant soil type in the *restinga* study area is the Quartzarenic Neosol (Sommer and Rosatelli 1991), recently formed by sediments of marine, lagoon and eolic accumulation (Quaternary Period). These soils are deep, predominantly sandy and well drained (Cabral 1999).

Sampling design and data collection

A total of 40 plots measuring 10 m × 10 m along existing trails were set up, 20 in Atlantic forest remnants and 20 in *restinga* remnants. All 20 plots of the Atlantic forest and 15 plots of *restinga* were set up in Lagoa do Peri Municipal Park; the remaining *restinga* plots were set up in Lagoa da Conceição Dunes Municipal Park (three plots) and Lagoa Pequena natural heritage site (two plots) (Fig. 1). This geographical separation of *restinga* plots was due to the limited area occupied by *restinga* remnants in the Lagoa do Peri Municipal Park. The minimum distance between plots was set at 20 m.

Samples of fertile and sterile terrestrial plants and hemi-epiphytes in direct contact with the soil were collected in each plot. The number of plants of each species was estimated for each plot. This estimation was based on counting the number of fronds of seven plants of each species outside the plots.The average value of frond number per species was then used as a denominator in the fraction of observed frond numbers for each species in the plots to estimate the number of plants of each species in the plots (Paciencia and Prado 2005).

The plant samples collected were identified, based on specialised bibliography for each family. The classification used follows PPG I (2016). Once identified, the plant samples were compared with existing material at FLOR (acronym follows Thiers 2019) and fertile material was deposited at the same herbarium.

All tree stems above 10 cm in circumference at ground level and the percentage of canopy cover were measured in each plot. Diameter at ground level (DGL) was then calculated from circumference measurements and percentage of canopy cover

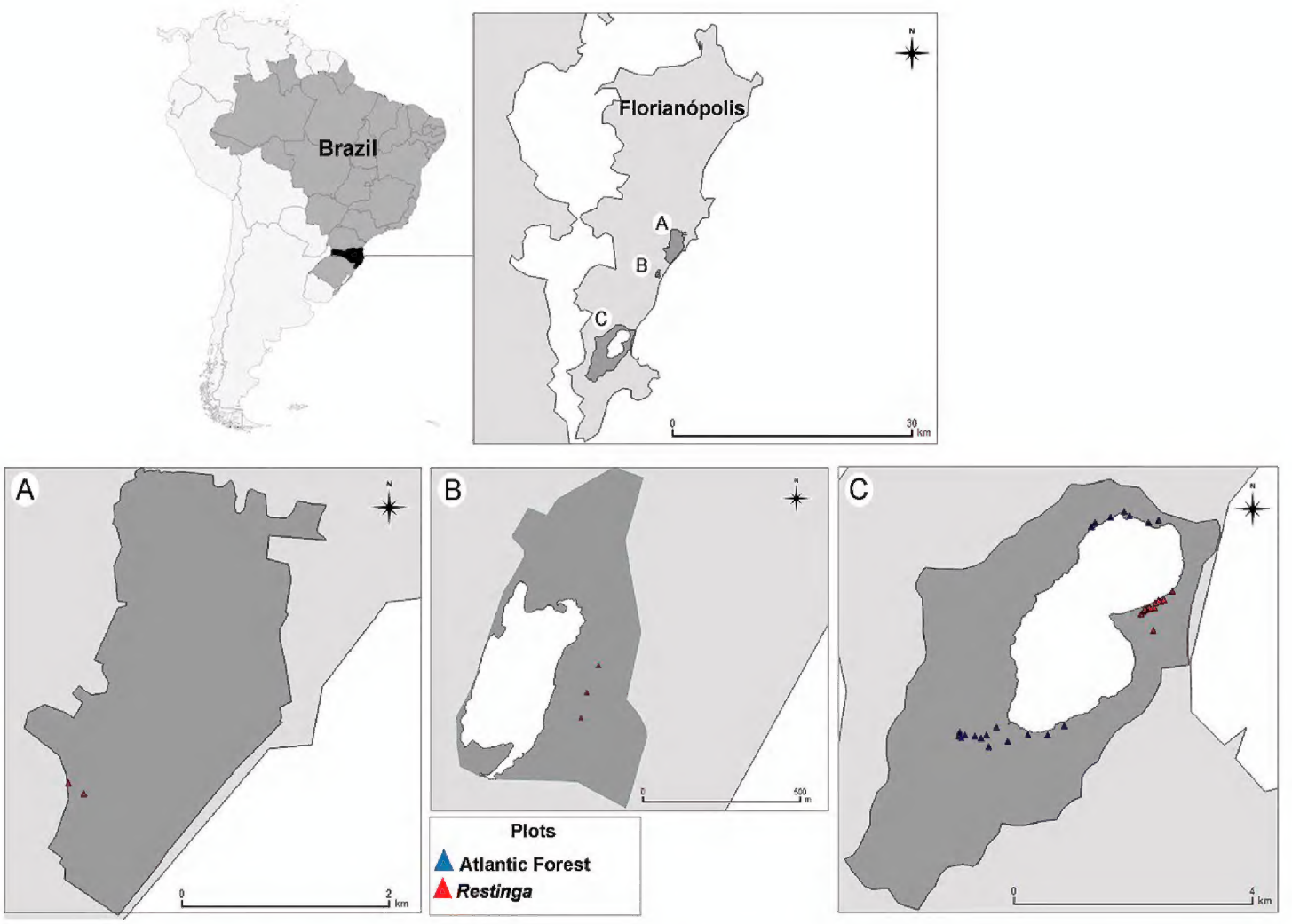

Figure 1. Location of the protected areas where the sampling plots were installed: (**A**) Lagoa da Conceição Dunes Municipal Park (**B**) Lagoa Pequena natural heritage site and (**C**) Lagoa do Peri Municipal Park (Florianopolis, Brazil). The location of each plot is represent by triangles in **A** to **C**.

was estimated from digital photographs taken with a Sony *Cyber-shot* camera. The camera was placed in the centre of each plot at ground level with the lens pointing upwards. Photographs were analysed with the Coral Point Count with Excel extensions (CPCe) software, version 4.1 (Kohler and Gill 2006) to derive the percentage of canopy cover in each plot.

Composite soil samples (500 g) were collected in each plot (subdivided in four quadrats) by mixing five subsamples (one per quadrat and one in the centre). All samples were taken from 0–20 cm depth after removal of litter. The soil samples were left to dry at room temperature for seven days or until completely dry (Donagema et al. 2011), then processed through a 2 mm mesh sieve and sent for analysis.

All physical analyses were conducted at the Water, Soil and Vegetable Tissue Laboratory of the Rural Engineering Department at the Agrarian Sciences Center of the Federal University of Santa Catarina. The physical analyses determined clay, sand and silt contents using the pipette method described by Donagema et al. (2011). The chemical analyses were conducted at the Soil Chemical Analyses Laboratory at EPAGRI (Santa Catarina Agricultural Research and Extension Agency). The parameters determined from the chemical analyses were effective acidity (pH) (soil to water ratio 1:1), potential acidity (H+Al), SMP index, organic matter (OM), available content of phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg),

aluminium (Al), cation exchange capacity (CEC) at pH 7, aluminium saturation (m), base saturation (V) and exchangeable cations, all analysed as described by Tedesco et al. (2004). Total organic carbon values (TOC) were obtained with the equation described by Donagema et al. (2011), based on organic matter values. In addition, flooding tendency was characterised in each plot as either periodically flooded soils or well drained dry soils, not subject to flooding.

Data analysis

A principal coordinates analysis (PCoA) (Gower 1966) was applied to ordinate the sampling plots in relation to the measured environmental variables (canopy cover and DGL, soil physical and chemical parameters, flooding tendency). Subsequently, a permutational multivariate analysis of variance (PERMANOVA) was used to test the nule hypothesis that environmental variables did not vary between the two vegetation types (999 permutations).

Generalised linear models (GLM) were used to compare species abundance, richness, diversity [Shannon-Wiener (H') and Simpson (D)] and dominance [Simpson index (1-D)] between vegetation types. While the Poisson distribution was assumed for richness and abundance variables, the Gamma distribution was assumed for species diversity and dominance indices, as well as edaphic and vegetation structure variables (canopy cover and DGL). The log link function was assumed for the relationship between the response and explanatory variables. The validation of each model was based on a graphical analysis of residuals. Species richness was estimated for the vegetation types using rarefaction curves (Chao estimator) and using interpolated and extrapolated data, based on the frequency of incidence of each species in the sampling plots (100 permutations; 10 sampling units for interpolation and 50 for extrapolation; 95% confidence interval).

The influence of soil characteristics, canopy cover and DGL on species composition of the sampled fern species was assessed using canonical correspondence analysis (CCA) (Ter Braak 1986). The matrix of environmental variables initially contained 17 variables, but eight of these were removed due to high redundance [VIF (variance inflation factor) > 4]. In order to test the significance of the influence of environmental variables on species composition based on abundance, Monte Carlo permutation tests (Ter Braak 1986) were carried out with 449 iterations.

The R software version 3.1.3 (R Core Team 2014) was used to process the statistical analyses using the *vegan* package (Oksanem et al. 2013) for the multivariate analysis (CCA, PCoA and PERMANOVA), while the 'iNEXT' (Chao et al. 2014) package was used to build the rarefaction curves for species richness.

Results

A total of 805 specimens were sampled, 520 in *restinga* and 285 in Atlantic forest. These plants were classified in eight families, 14 genera and 14 species (Suppl. ma-

terial 1: Table S1). Eight of the total number of species were collected exclusively in *restinga*, five exclusively in Atlantic forest and two in both vegetation types (Suppl. material 1: Table S1). All sampled species belong to the Polypodiopsida (Smith et al. 2006).

The families with higher richness in *restinga* were Blechnaceae, Polypodiaceae and Pteridaceae, each represented by two species. Blechnaceae was the most abundant (192 plants) due to the high density of *Telmatoblechnum serrulatum* in the plots where it occurred, especially in areas prone to flooding. The family best represented in Atlantic forest, both in number of species and number of plants, was Pteridaceae (three species, 151 plants). Two of the three most abundant species in Atlantic forest (*Adiantum pentadactylon*, *Anemia phyllitidis* and *Doryopteris pentagona*) belong to this family (Suppl. material 1: Table S1).

The first two axes of the PCoA explained 62.6%of the explained variation (PCoA 1: 36.1% and PCoA 2: 26.5%). There was a clear distinction between the two vegetation types in terms of the environmental variables measured (Fig. 2). This distinction was evidenced by the result of the PERMANOVA ($F = 13.12$, $R^2 = 0.26$, $p = 0.001$). The *restinga* plots showed a greater variation in environmental variables than those of Atlantic Forest, especially due to flooding tendency where all periodically flooded plots were in *restinga* (Fig. 2, Suppl. material 1: Table S2).

No significant difference was found between the vegetation types in terms of species richness, diversity, [Simpson (D) and Shannon-Wiener (H') indices] or dominance [Simpson index (1-D)] (Table 1). Abundance was higher in *restinga* than in Atlantic forest ($P < 0.001$; Table 1). The rarefaction curves did not show any differences in species richness between vegetation types (Fig. 3). The Atlantic forest curve, however, showed a tendency for stabilisation, while the *restinga* curve continued to rise, indicating that a larger number of species would have been registered had the number of plots been increased.

The canonical correspondence analysis showed that 53.67% of the variation in the species matrix was explained by the environmental variables used in the analysis. The first two axes represented 55.85% of the explained variation (CCA 1: 28.69% and CCA 2: 27.16%, Table 2, Fig. 3). Besides, the Monte Carlo permutation test showed significant correlations between species abundance and most of the environmental variables ($p < 0.05$) (Table 3). The variables, more strongly correlated with the first axis of the CCA, were average DGL and flooding tendency, followed by aluminium concentration (Al) and sand percentage (Table 3). The variables more correlated with the second axis were, in decreasing order, calcium concentration (Ca), clay content and canopy cover (Table 3).

Two separate groups were distinguished by plot ordination (Fig. 4A). The first one was composed by *restinga* plots associated with high sand content and aluminium concentration (Al). The second group was composed by Atlantic forest plots on soils with higher calcium concentration, higher clay content and canopy cover. One of the *restinga* plots was not ordinated with the rest, which seems to be primarily explained by the presence of trees with larger DGL values and flooding (Fig. 4A).

Table 1. Average values (±SE) of species abundance, richness, diversity [Shannon-Wiener (H') and Simpson (D)] and dominance [Simpson (1-D)] in plots in remnants of Atlantic forest (AF) (n = 20) and *restinga* (RF) (n = 20). *P* values refer to generalised linear models realised for each variable for comparison between the two vegetation types. Significant *P* values are indicated with an asterisk.

	RF	AF	
	Average (±SE)	**Average (±SE)**	***P***
Abundance	26 (±16.31)	14.25 (±18.04)	<0.001*
Richness	2.30 (±1.03)	2.05 (±0.82)	0.59
Shannon-Wiener (H')	0.477 (±0.35)	0.480 (±0.36)	0.98
Simpson (D)	0.289 (±0.22)	0.307 (±0.23)	0.81
Simpson (1-D)	0.710 (±0.22)	0.693 (±0.24)	0.81

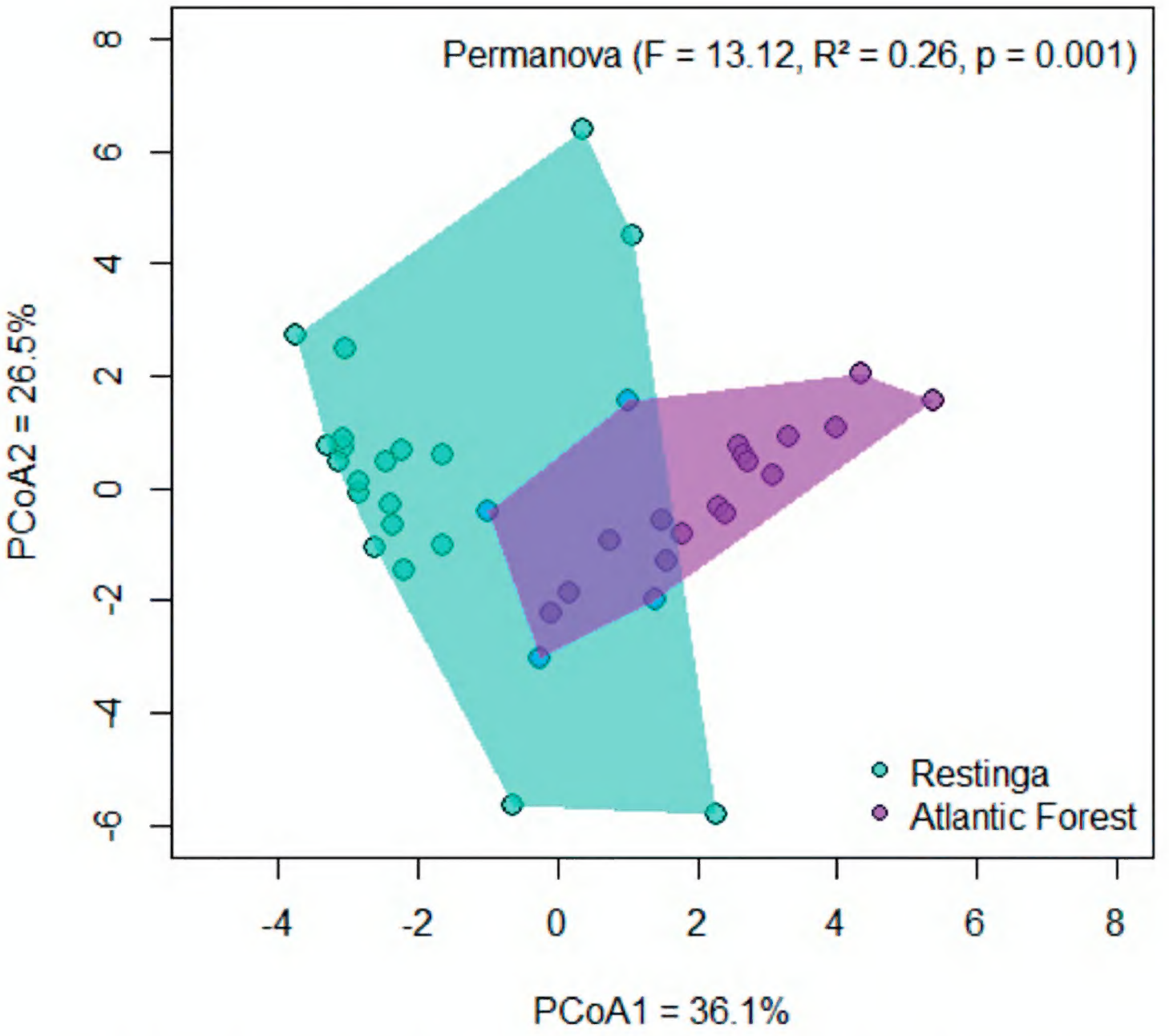

Figure 2. Representation of the principal coordinates analysis (PCoA) and result of the permutational multivariate analysis of variance (PERMANOVA) for environmental variables (canopy cover and DGL, soil physical and chemical parameters, flooding tendency) measured in 40 plots in remnants of Atlantic forest (n = 20) and *restinga* (n = 20).

Table 2. Eigenvalues of the CCA axes and the proportion of variation explained by each of the axes.

	Eigenvalue	Proportion explained
Axis 1	0.9022	0.2869
Axis 2	0.8540	0.2716
Axis 3	0.6405	0.2037
Axis 4	0.3361	0.1069
Axis 5	0.1928	0.0613
Axis 6	0.1573	0.0500
Axis 7	0.0484	0.0154
Axis 8	0.0122	0.0038
Axis 9	0.0012	0.0004

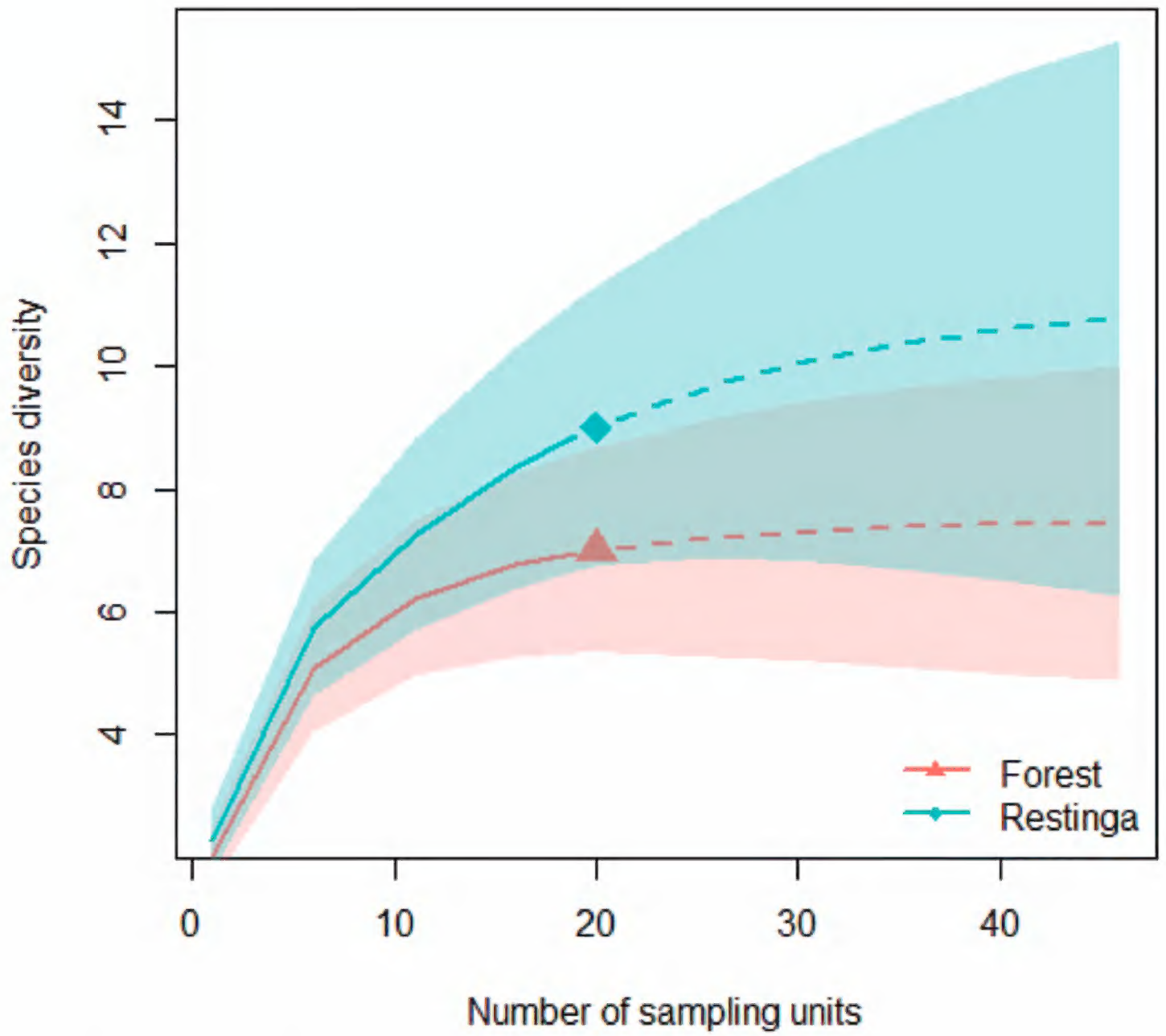

Figure 3. Species rarefaction curves generated from 50 permutations, based on the incidence frequency of each species in the sampled plots in remnants of Atlantic forest (AF) (n = 20) and *restinga* (RF) (n = 20). Full lines represent data interpolation (up to 20 plots for each vegetation type) and dashed lines represent data extrapolation. Lighter coloured areas indicate a 95% confidence interval.

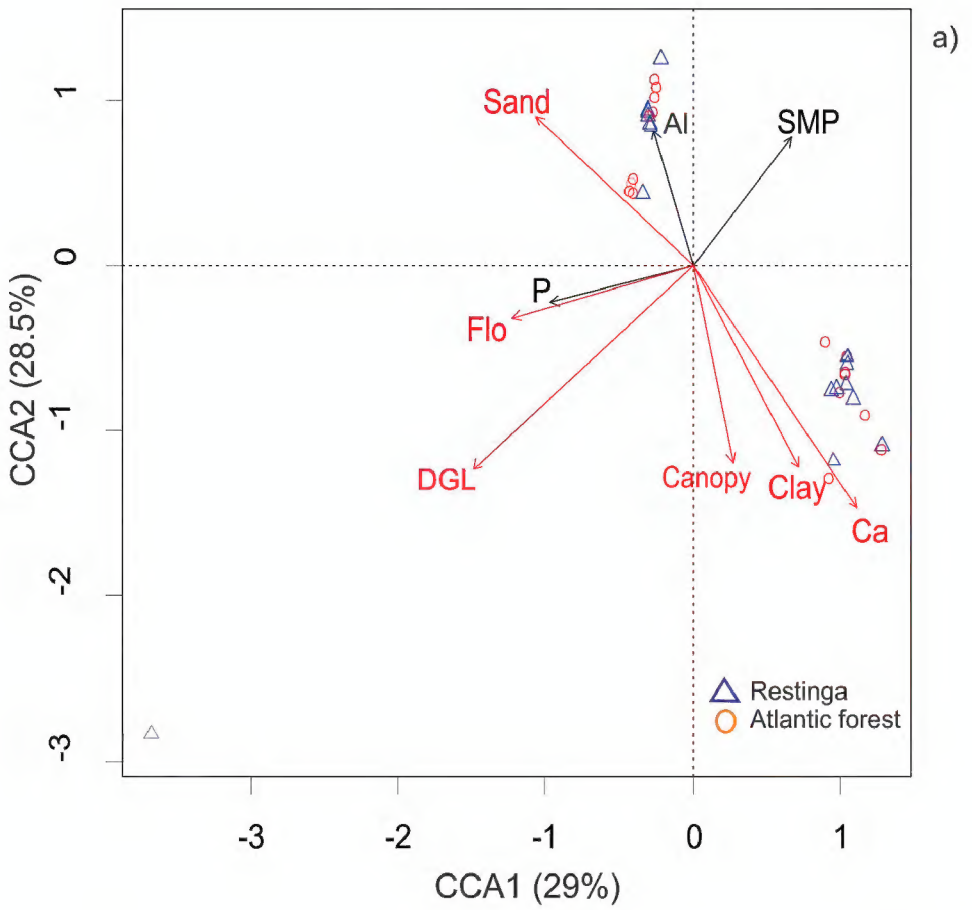

Figure 4. Plot (**a**) and species (**b**) ordination from plots in remnants of Atlantic forest (n = 20) and *restinga* (n = 20) and their correlation with nine abiotic variables [aluminium (Al), calcium (Ca), canopy cover, clay (%), flooding (Flo), ground level diameter (DGL), index SMP (SMP), phosphorus (P), sand (%)]. The axes show the percentage of variation explained by the constraining variables. The nine variables showed significant correlation with data variance ($p \leq 0.05$) according to the Monte Carlo permutation test, but just those in red were not redundant [VIF (variance inflation factor) < 4]. Sampled species were: A. pen: *Adiantum pentadactylon*; A. phy: *Anemia phyllitidis*; A. ser: *Asplenium serra*; C. pha: *Cyathea phalerata*; D. pen: *Doryopteris pentagona*; L. eff: *Lastreopsis effusa*; N. bra: *Neoblechnum brasiliense*; P. lep: *Pleopeltis lepidopteris*; P. cyl: *Polybotrya cylindrica*; P. ara: *Pteridium arachnoideum*; P. den: *Pteris denticulata*; R. adi: *Rumohra adiantiformis*; S. lat: *Serpocaulon latipes*; T. ser: *Telmatoblechnum serrulatum*.

Table 3. Environmental variables used in Canonic Correspondence Analysis (CCA), their correlations with ordination axes and significance in species abundance (Monte Carlo test) in plots in remnants of Atlantic forest (n = 20) and *restinga* (n = 20). Al: aluminium content; Ca: calcium content; Canopy: percentage of canopy cover; Clay: percentage of clay; Flooding: flooding tendency; Mean DGL: mean ground level diameter; P: phosphorus content; Sand: percentage of sand; SMP: index SMP. Significant *P* values are indicated with an asterisk.

Parameters	Correlations						*P*
	CCA 1	CCA 2	CCA 3	CCA 4	CCA 5	CCA 6	
Flooding	-0.5854	-0.1514	0.5679	-0.1525	-0.1651	0.0857	0.04*
Sand (%)	-0.5074	0.4337	0.2593	-0.4490	-0.1517	0.0075	0.001*
Clay (%)	0.3426	-0.5834	0.2713	-0.2441	0.2533	0.2521	0.001*
P (mg/dm³)	-0.4618	-0.1072	0.3669	-0.1635	-0.0685	0.0850	0.04*
SMP	0.3236	0.3728	-0.4166	-0.2047	0.0018	0.5098	0.07
Al (cmolc/d)	-0.1265	0.3934	-0.0248	0.1723	0.3009	0.1934	0.16
Ca (cmolc/d)	0.5334	-0.6994	0.0864	-0.0669	-0.0312	0.3301	0.001*
Canopy (%)	0.1318	-0.5689	0.0258	-0.0334	-0.6813	-0.1437	0.01*
Mean DGL	-0.7116	-0.5891	-0.0410	-0.2421	0.2138	-0.0258	0.001*

The ordination of species, based on edaphic variables and on vegetation structure variables, showed that *Telmatoblechnum serrulatum*, *Pleopeltis lepidopteris* and *Rumohra adiantiformis* occurred in plots with sandy soils, lower calcium concentration and higher aluminium concentration (Fig. 4B, Suppl. material 1: Table S2, Table S3). The species *Adiantum pentadactylon*, *Anemia phyllitidis*, *Doryopteris pentagona*, *Lastreopsis effusa* and *Pteris denticulata* occurred on soils with higher clay content, higher calcium concentration and higher canopy cover (Fig. 4B, Suppl. material 1: Table S2). *Neoblechnum brasiliense* and *Serpocaulon latipes* occurred in both vegetation types. The first was more abundant on soils with higher clay content while the second species was more abundant on soils with higher sand content (Fig. 4B, Suppl. material 1: Table S2, Table S3). *Asplenium serra*, *Cyathea phalerata* and *Polybotrya cylindrica* were more frequent on sites with tendency to flooding, higher phosphorus content and higher DGL values (Fig. 4B, Suppl. material 1: Table S2, Table S3).

Discussion

The observed differences in edaphic conditions and vegetation structure in general was followed by differences in fern abundance and species composition between the vegetation types in this study. While soils in Atlantic forest contained higher cation availability, such as calcium, soils in *restinga* contained lower cation availability and higher aluminium concentration. Different edaphic conditions, therefore, enable the establishment of some species to the detriment of others. Well drained soils in *restinga* favour *P. lepidopteris*, *R. adiantiformis* and *S. latipes*, as already observed by Korte et al. (2013). Conversely, *T. serrulatum*, *C. phalerata*, *P. cylindrica* and *A. serra* predominate in flooded areas and are common in swamp forests (Magnano et al. 2010; Gonzatti et al. 2014). Flooding events increase the availability of phosphorus as a consequence of the hydrolysis of iron and aluminium phosphates (Souza et al. 2012). Flooding con-

ditions in some areas of *restinga* may therefore facilitate the establishment of species that grow in more specific habitats, such as *P. cylindrica* and *C. phalerata*. The first occurs principally in Atlantic forest, serving as an indicator of this vegetation type (Nóbrega et al. 2011), while the second species occurs in areas with high phosphorus content (Coomes et al. 2005), which is common in forests subjected to flooding.

The existence of flooded and non-flooded habitats in *restinga* produces a greater variety of habitats, facilitating the co-existence of species with different environmental tolerance (Gonzatti et al. 2014). As a consequence, despite more restrictive edaphic conditions in *restinga* (soils poorer in nutrients and higher in aluminium concentration), no differences were found in species richness and diversity between *restinga* and Atlantic forest. Similar results have been found in other studies in which the richness of ferns was compared in areas with soils of different textures (Young and Leon 1989; Tuomisto and Ruokolainen 1993) and cation availability along edaphic gradients (Tuomisto et al. 2002).

Although species richness and diversity did not differ between vegetation types, fern abundance was higher in *restinga*, which was explained by the dominance of *T. serrulatum* and *R. adiantiformis* in some of the plots. The first was very abundant in periodically flooded soils, while the second occurred in higher abundance on well drained soils (Magnano et al. 2010; Korte et al. 2013). These two species have morpho-physiological characteristics that probably enable their survival in the restrictive conditions of *restinga*. *Rumohra adiantiformis*, for example, can survive in areas of high incidence of light and low water availability due to reduced leaf area, greater mesophyll thickness and frond inclination (Boeger et al. 2007), while smaller size and higher frequency of stomata enable the survival of *T. serrulatum* in flooded areas (Rolleri et al. 2010).

Canopy cover and DGL also determined the differences observed in species composition between vegetation types. *Rumohra adiantiformis* was more abundant in areas with lower canopy cover, while *A. pentadactylon*, *A. phyllitidis*, *D. pentagona* and *L. effusa* were more abundant in more shaded areas. These results corroborate information already described in scientific literature for *R. adiantiformis*. This species has a wide geographic distribution, occurring from open *restinga* to temperate *Araucaria* forests (Korte et al. 2013; Gasper and Salino 2015), being more abundant along forest borders or in clearings (Korte et al. 2013). On the other hand, *A. pentadactylon*, *A. phyllitidis* and *D. pentagona*, mainly found in shaded areas, do not corroborate evidence from other studies, which indicate that these species thrive along trails and river margins, cut slopes along roads and areas exposed to solar radiation (Boldrin and Prado 2007; Winter et al. 2011). The discrepancy between our results and previous studies may be due to an isolated effect and/or association of edaphic conditions, which could have overcome the independent effect of canopy cover.

High DGL values, in association with higher canopy cover, probably favoured the establishment of more shade tolerant species in *restinga*, such as *P. cylindrica*. As forests in advanced successional stages provide more shade, the establishment of species with low tolerance to direct solar radiation is favoured. According to Moran (1987), *Polybotrya* occurs preferably in shaded areas in mature forests, rarely growing

in disturbed sites. In Brazil, *P. cylindrica* is mainly found inside mature Atlantic forest formations (Canestraro and Labiak 2015), being less common along trail margins (Hirai and Prado 2012) and in *restinga* (Nóbrega et al. 2011; Gonzatti et al. 2014).

The fern community seems to respond to variations in edaphic conditions and vegetation structure of the vegetation types compared in this study, in which the soil plays a predominant role. Different soil conditions of texture, fertility and drainage influence species composition. Aluminium content in the soil also seems to be important for the establishment of some terrestrial or hemi-epiphytic fern species. A greater variety of habitats due to differences in soil drainage in *restinga* tends to facilitate the co-existence of species with different levels of ecological tolerance, compensating for limiting conditions (low cation availability and high aluminium concentration), typical of this vegetation type.

The heterogeneity of habitats and environmental conditions which exists not only between vegetation types, but also within types, was an important factor in the differentiation of species composition, also showing the exclusivity of species to certain abiotic conditions. Therefore, habitat heterogeneity must be taken into account in conservation strategies aimed at the protection of a large number of species in this biodiversity hotspot.

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Supplementary material 1

Tables S1–S3

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Data type: species data

Explanation note: **Table S1.** List of terrestrial and hemiepiphytic species sampled in 40 plots of Atlantic forest and *restinga*. Vegetation types – AF: Atlantic forest; RF: *Restinga*. Habitat- PF: periodically flooded soils; WD: well drained, dry soils not subject to flooding. Life form: Hm: hemiepiphyte; Tr: terrestrial. Protected area - LCDMP: Lagoa da Conceição Dunes Municipal Park; LP: Lagoa Pequena; LPMP: Lagoa do Peri Municipal Park. **Table S2.** Biotic and abiotic data of plots set up in remmants of Atlantic forest (AF) (n=20) and *restinga* (RF) (n=20) (Florianópolis, Santa Catarina, Brazil). **Table S3.** Biotic data of plots set up in remmants of Atlantic forest (AF) (n=20) and *restinga* (RF) (n=20) (Florianópolis, Santa Catarina, Brazil).

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